

THE LARVA AND PUPA OF *SCHIZONYXHELEA FORATTINII* WIRTH AND GROGAN (DIPTERA: CERATOPOGONIDAE) WITH A DISCUSSION OF THE PHYLOGENETIC RELATIONSHIPS OF THE GENUS

ART BORKENT

Research Associate, Royal British Columbia Museum and the American Museum of Natural History, 1171 Mallory Road, R1-S20-C43, Enderby, British Columbia, V0E 1V0, Canada (e-mail: aborkent@jetstream.net)

Abstract.—The larva and pupa of *Schizonyxhelea forattinii* Wirth and Grogan are described for the first time. Larval, pupal and adult character states suggest that this genus is closely related to *Stilobezzia* Kieffer and may even be most closely related to only some species of *Stilobezzia*.

Resumen.—Se describen por primera vez larva y pupa de *Schizonyxhelea forattinii* Wirth y Grogan. El estado de los caracteres de larva, pupa y adulto, sugiere que este género se halla muy relacionado a *Stilobezzia* Kieffer, y puede aún, ser más cercano a sólo algunas especies de *Stilobezzia*.

Key Words: *Schizonyxhelea*, *Stilobezzia*, immatures, taxonomy, phylogeny, systematics, Costa Rica, Neotropical

The immatures of the Ceratopogonidae remain as one of the most poorly known life stages of all nematoceran families. As part of a project to generate descriptions, keys and phylogenetic interpretation of these stages (Borkent, in preparation), this paper provides a description of the larva and pupa of *Schizonyxhelea forattinii* Wirth and Grogan and interprets available character stages of the genus *Schizonyxhelea* Clastrier from a cladistic perspective.

Schizonyxhelea includes two Neotropical species and both are very small in size, with wing lengths of 0.7–0.8 mm. When the genus was first proposed by Clastrier (1984), he suggested that the single known species, *S. guyana*, was similar to species of *Nannohelea* Grogan and Wirth and *Bothahelea* Grogan and Wirth. Wirth and Grogan (1988) described a second species, *S. forattinii*, including the first male of the genus and hypothesized that *Schizonyxhelea* was

related to a group of genera with reduced features: *Baeohelea* Wirth and Blanton, *Baeodasymyia* Clastrier and Raccurt, *Nannohelea* Grogan and Wirth and *Rhynchohelea* Wirth and Blanton. Since then Borkent (1992, 1995), Borkent and Craig (1999) and Grogan and Borkent (1992) have shown that *Baeohelea* and *Baeodasymyia*, as sister genera, are likely an early lineage within the Ceratopogonini and that *Nannohelea* and *Rhynchohelea* belong to a group which also includes the genera *Brachypogon* Kieffer, *Ceratoculicoides* Wirth and Ratanaworabhan and *Sinhalohelea* Grogan and Borkent. The genus *Schizonyxhelea* has remained an enigma. Discovery of the immatures and examination of fresh adult material of *S. forattinii* provided an opportunity to further investigate the genus.

MATERIALS AND METHODS

Terms for larval and pupal structures follow Lawson (1951). The single live larva

was discovered by placing a mud sample in water and shaking the container gently. The swimming larva was then captured with an eye-dropper and reared in a petri dish (5 cm in diameter) with a small amount of substrate (mud and detritus) from the original habitat. The larva and subsequent pupa were kept at ambient temperature (approximately 25°C) and checked daily. When needed, a small amount of water was added to the petri dish to keep the sample from drying. The larval and pupal exuviae and partially emerged adult were preserved in 70% ethanol and slide-mounted using the method described by Borkent and Bissett (1990).

Adults were also captured in the field by sweeping vegetation with an aerial net; these were examined as cleared specimens in glycerine and on slides. Specimens were compared to the holotype of *S. forattinii*.

The specimens are deposited in the Canadian National Collection in Ottawa, Ontario, Canada.

DESCRIPTION OF LARVA AND PUPA

Fourth instar larva.—Body length unknown. Head capsule (Figs. 1A, B) relatively short (111 μm), blunt (head length/width = 1.28), uniformly medium brown. Collar slightly darker than rest of head capsule, well-developed ventrally with ventrolateral anterior apodeme, separated ventromedially, terminating dorsolaterally. Frontal suture extending to near anterior margin of labrum. Ventral suture short. Most setae simple with the following divided or plumose: s, v, posterior o; arrangement as in Figs. 1A, B; bases of sensilla more or else equal in size; following sensilla not visible: j, r, z, x, n. Antenna short, further details not visible. Eye unknown. Labrum short, wide, details not visible. Mandible elongate, basal portion straight, apical third curved, sensilla not visible. Maxilla not clearly visible, palpus short. Hypostoma a broadly rounded projection. Epipharynx with 1 pair of serrate combs, divided medially (Fig. 1B). Thorax, abdomen with

more or less uniform light pink pigmentation. Caudal segment, anal papillae unknown.

Pupa.—Length 1.29 mm. General coloration uniformly light brown. Body surface generally smooth with only a few tubercles and spicules associated with setae, a few restricted to the medioanterodorsal and medioanteroventral areas of abdominal segments 3–8 and anal segment. Operculum (Fig. 1C) with well-developed anteromarginal seta located on tubercle, with pore at tubercle base; dorsolateral margin with row of well-developed spines. One well-developed anterodorsal seta on moderately elongate, rounded tubercle (Fig. 1G). One long, slender and two shorter dorsolateral setae (Fig. 1H). Two short dorsomedial setae, one thicker than other (Fig. 1F). Five dorsal sensilla, i short thick seta, ii, iv short, slender setae, v, vi pores; i, ii, iv on single, rounded, short, separate tubercles (Fig. 2A). Ventromedian setae not visible (if present, they are very minute). Two ventrolateral setae slender, bases somewhat separate (Fig. 1E). Respiratory organ (Fig. 1D) somewhat curved, smooth; four spiracles situated along length, with 5–6 spiracles situated apically, opening at surface; tracheal tube of more or less equal diameter for length. Metathorax not divided medially, with medial protuberance from scutum protruding to near posterior margin. Abdomen with setae separate from one another (none on common tubercle), each bordered by comb-like or single elongate spicules. Segment 4 setal pattern (Fig. 2C) with 2 d.a.s.m., 4 d.p.m., 1 l.a.s.m., 3 l.p.m., 3 vn; setae d.p.m. i–iii not present or very small; setae d.p.m. iv, l.a.s.m., l.p.m. i, iii, all thick, stout. Anal segment (Fig. 2B) with caudal spine moderately elongate, somewhat curved apically, directed posterolaterally.

Bionomics.—The single larva was collected on December 17, 1993, 2 km north-east of Tarcoles, Costa Rica from wet mud in a small seep which flowed into the outflow of a larger spring on private property directly west of Reserva Carara. The larva

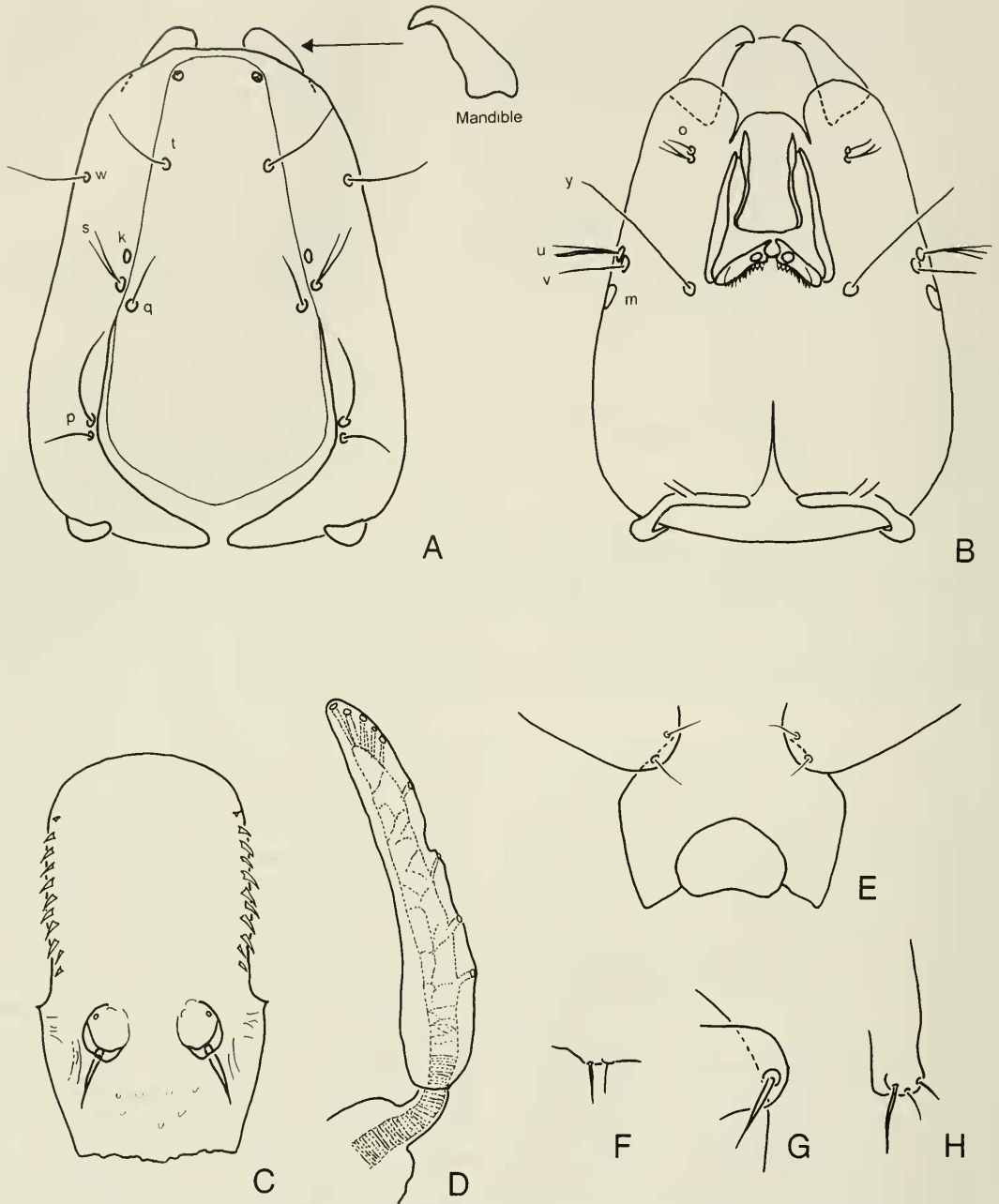


Fig. 1. Structures of *Schizonyxhelea forattinii*. A, Larval head capsule in dorsal view. B, Larval head capsule in ventral view. C, Pupal operculum. D, Pupal respiratory organ. E, Pupal mouthparts in ventral view. F, Pupal dorsomedial setae. G, Pupal anterodorsal seta. H, Pupal dorsolateral setae.

swam with the same rapid serpentine motion as do so many Ceratopogoninae. During eight months in Costa Rica (July, 1993–Feb. 1994) I collected only one larva and

two male and 11 female adult *S. forattinii*. Each of the sites was at, or very near, a first order seep or spring, or a small stream and specimens were collected from August to

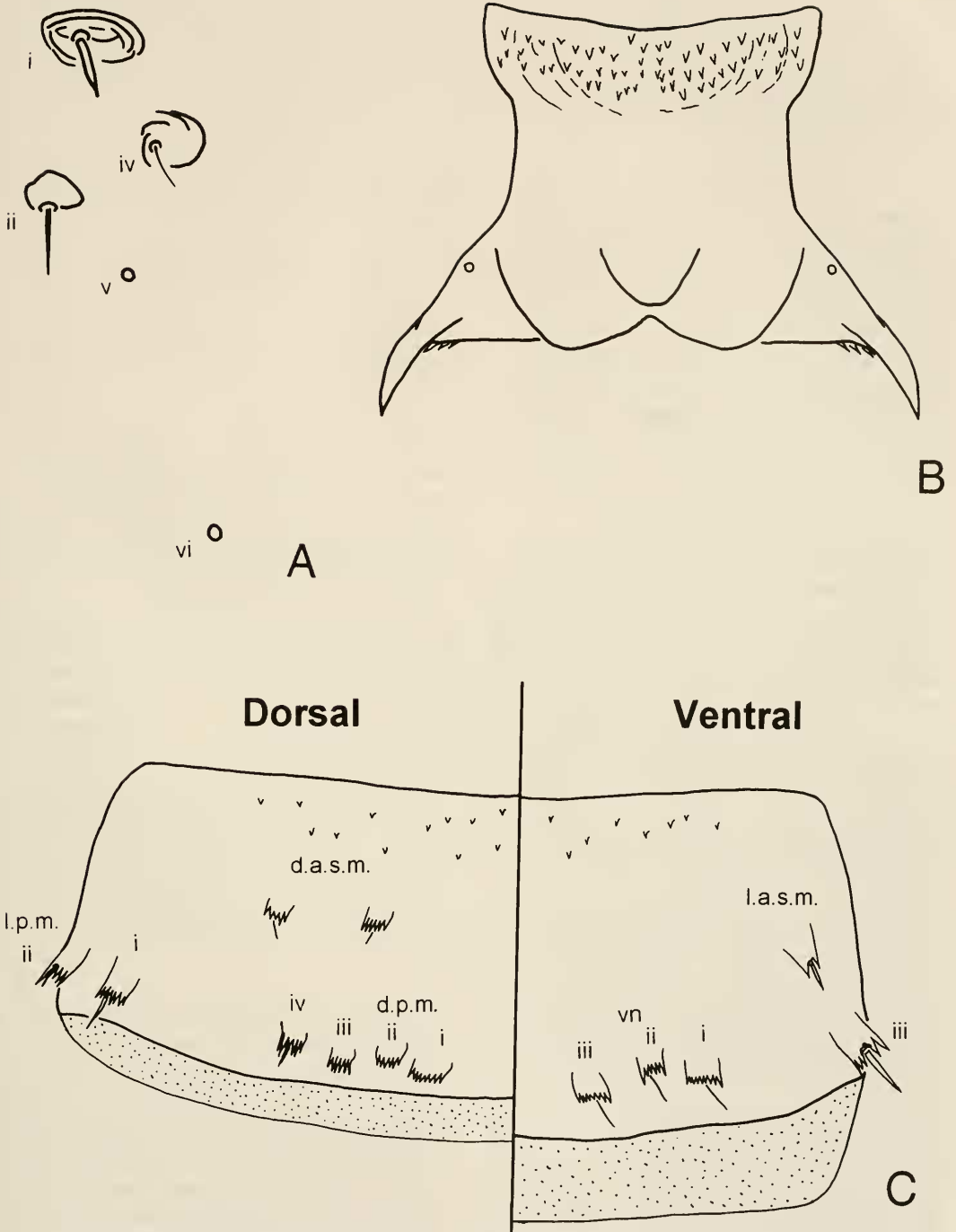


Fig. 2. Pupal structures of *Schizonyxhelea forattinii*. A, Dorsal setae. B, Anal segment in ventral view. C, Setae of fourth abdominal segment.

December (3 sites at 2 km NE Tarcoles from Aug. 3 to Dec. 17, 1993; a first order spring in Atenas Oct. 1 to Dec. 7, 1993). This suggests that immatures of this species are restricted to small lotic habitats.

DISCUSSION

There are two newly discovered character states which provide cladistic information regarding the phylogenetic position of *Schizonyxhelea*. The first is the presence of plumose setae on the head capsule of the larva, which merely indicates the unsurprising conclusion that this taxon belongs within that group of Ceratopogoninae which is the sister group of *Ceratopogon* Meigen and, possibly *Baeodasymyia* + *Baeohelea*. This character is discussed further by Borkent and Craig (1999). The second character state concerns the nature of the male aedeagus. Borkent (1995: 97–98) discussed (as his character 39) the uniquely divided aedeagus of species of *Stilobezzia* Kieffer. Wirth and Grogan (1988) pointed out that the male aedeagus of *Schizonyxhelea* was difficult to interpret. However, re-examination of fresh material here, especially from a posterior aspect, shows that the aedeagus of *S. forattinii* is divided medially, indicating at least a sister group relationship to, or within, *Stilobezzia*.

Further character states suggest that *Schizonyxhelea* is actually closely related to a species group within *Stilobezzia* and they are discussed below. Although these features are not yet understood cladistically, continuing studies show promise for the interpretation of most of these (Borkent, in preparation).

—Larval head capsule sensilla q, s, k are all close to each other (present in *Stilobezzia flavirostris* (Winnertz) and *S. papillata* Remm, the only two species of *Stilobezzia* for which this character state has been described). The character state appears to be unique within the Ceratopogonini but is also present in some Sphaeromiini and Palpomyiini.

—The following features are shared with

the pupa of *Stilobezzia bulla* Thomsen: pupal respiratory organ shape and distribution of spiracles virtually identical; presence of thick spines on margin of operculum (also present in many other genera); same number and similar size of thoracic setae; specific distribution of sensilla and spines on segment 4 especially including the anterior lateral sensilla and the presence of comb-like spines associated with most sensilla very similar; presence of two medial, low projections on the dorsum of the anal segment; presence of spines on posterior margin of apicolateral processes of anal segment.

—All *Stilobezzia* pupae are missing one of the dorsal setae (probably # 3) and this appears to be nearly unique within the Ceratopogonidae. It is also known in *Baeodasymyia*; Borkent and Craig (1999) misidentified sensilla v as iii and vi as v.

—The male antenna of *Schizonyxhelea* have flagellomeres 5–10 fused. Flagellomeres 5–9 are fused in *S. bulla* and flagellomeres 5–10 in *S. thomsenae* Wirth. The males of most species of *Stilobezzia* have separate flagellomeres.

—A few genera of Ceratopogonini (including *Stilobezzia*) and most genera of Heteromyiini + Sphaeromiini + Palpomyiini + Stenoxenini have a secondary row of palisade setae (defined in detail by Borkent, in press). This is also present in *Schizonyxhelea*.

—Adult eyes of *Schizonyxhelea* have minute interfacetal pubescence. Very small interfacetal spicules are also present in *S. bulla* (otherwise rare in *Stilobezzia*).

—Wing with radial cells reduced. Although Wirth and Grogan (1988) suggested that *Schizonyxhelea* lack radial cells, the male I have had a narrow second radial cell. A number of *Stilobezzia* species have a small or completely reduced first radial cell. However, loss of radial cells is known in a number of other genera of Ceratopogonidae and the character state cannot be interpreted at present. It was likely the reduced radial cells which led Wirth and Grogan (1988) to

suggest that *Schizonyxhelea* was related to other genera with reduced wing venation but, as noted in the introduction, these taxa with reduced character states are not closely related to one another. It is apparent that several lineages of Ceratopogonidae have produced small species which have independently reduced their wing venation and, for some, their mouthparts, antennae and parts of the male genitalia.

—Wing with a narrow apical band of macrotrichia. This character state is shared with *S. bulla* and *S. thomsenae* and appears to be unique with the subgenus *Stilobezzia*. Members of the subgenera *Debenhamia* Wirth and Grogan and *Acanthohelea* also have macrotrichia on the wing membrane but this is nearly always more generally distributed on the apex of the wing. *Stilobezzia* (*Acanthohelea*) *insolita* Das Gupta and Wirth from Malaysia also has a narrow band of macrotrichia and the female has a distinctively (but not unique within the Ceratopogonidae) curved single spermathecae very similar to that present in female *Schizonyxhelea*.

—Aedeagus very reduced in size. This character state is shared with *S. bulla*, *S. thomsenae* and a few other *Stilobezzia*. The condition is otherwise rare within the Ceratopogonidae.

—Male cerci are closely approximated. This is present in *S. thomsenae*, some other *Stilobezzia* and some other genera of Ceratopogonini.

The striking similarity of the pupae of *Schizonyxhelea forattinii* and *Stilobezzia bulla* and the presence of fusion of male flagellomeres 5–9 or 10, the narrow band of apical of macrotrichia on the wing and the reduced aedeagus shared with *S. bulla* and *S. thomsenae* probably indicates that the two species of *Schizonyxhelea* are actually small *Stilobezzia* with a somewhat reduced wing venation and with equal claws on each leg of the female. A reversion from a single claw to double claws is known in other genera such as *Serromyia* Meigen (Borkent and Bissett, 1990) and *Alluau-*

myia Kieffer (personal observation of new species) and it would not be surprising to find the same within *Stilobezzia*; indeed, I have a small *Stilobezzia* from Costa Rica with equal claws but with typical *Stilobezzia*-like wing venation (i.e., a small first and a long second radial cell is present).

It is yet possible that the pupal character states shared by *Schizonyxhelea forattinii* and *Stilobezzia bulla* are plesiomorphic within *Stilobezzia* and that *Schizonyxhelea* is therefore the sister group of *Stilobezzia*. Further study is required of character state polarities to resolve this question (Borkent, in preparation). For the present it is best to continue to recognize *Schizonyxhelea* as a valid genus.

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